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THE GENERA OF THE ENCHYTRAEIDAE (OLIGOCHAETA)[1]

BY PAUL S. WELCH

INTRODUCTION

Michaelsen's monograph (1900) on the Oligochaeta contains the last general revision of the genera of the Enchytraeidae for the whole world. Eisen (1905) modified, to some extent, the genera then known to occur in North America. Since the publication of the above-mentioned works numerous contributions to the knowledge of these annelids have been made, so that the family has grown from a relatively small group containing 13 genera and less than 100 species to the present status of 16 genera and approximately 325 species. With this marked increase has come the necessity for certain changes and modifications in the limits of most of the groups.

The revision herein presented is the direct result of the discovery of certain enchytraeids which failed to agree exactly with any of the older generic descriptions and in order to properly assign them a careful survey of several genera was necessitated. It was then decided to extend the study to include all of the known genera of Enchytraeidae and thus not only make available a considerable amount of inaccessible material but also present something which will serve as a basis for further revision as soon as more data are secured. The writer wishes to acknowledge indebtedness to one of his graduate students, Miss Helen M. Scott, who gave considerable assistance in testing and rechecking the revised generic descriptions.

This revision can at best be regarded only as an attempt to indicate progress to date. Certain unsurmountable difficulties make it impossible at the present time to do more than work over critically the published records as they now stand and to determine the present status of each group as nearly as possible. The descriptions of all of the species now assigned to the Enchytraeidae (approximately 325) have been re-examined in this connection and the work of the writer on this group of annelids, covering a period of ten years, has been brought to bear upon the task wherever possible. The principal difficulties are indicated below in order to point out some of the features which should receive attention in future investigations and revisions:

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[1] Contribution from the Zoological Laboratory of the University of Michigan.

1. Descriptions based upon sexually immature specimens or upon material not so stated but apparently immature.
2. Species placed tentatively in certain genera but data insufficient to make final disposal of them.
3. Lack of information on morphological features now known to have important systematic value, especially in the older descriptions
4. Deviations which strongly have the appearance of being errors of observation or of printing.
5. Structures recorded as "not seen" or "not found" sometimes the result of faulty methods of study, such as external examination only or dissection only, or the use of poorly preserved specimens.
6. Difficulty in correct interpretation of certain descriptive terms, as for example, does "lobulated testes" mean *divided* testes as represented in *Lumbricillus* or something much less significant. In the absence of illustrations which supplement the descriptions, such expressions are very puzzling.
7. Interpretation of indefinite terms indicating differences of degree, as for example, "setae slightly curved," an expression which when unaccompanied by further explanation or by figures is practically unusable.
8. Difficulty arising from descriptions which fail to mention important organs. Does lack of mention always or ever mean positive absence of the structure? Apparently, many investigators have not realized the importance of stating *positively* that certain characters are absent. To leave these matters without mention is a distinct detriment.

In this revision, the generic descriptions have been so modified as to include what seems to be well founded changes demanded by increased data as well as new features now regarded as having generic value. In making these modifications the procedure has been as follows:

1. The writer concurs with those who hold that the multiplication of genera should be avoided except where the case is perfectly clear.
2. Genera and species founded upon sexually immature material have been disregarded. It is well established that complete, depend-

able data cannot be secured from immature specimens and it is to be hoped that future investigation will frown upon any disposition to write descriptions from such imperfect material. It can only lead to confusion and hinderance.

3. Data easily derivable from illustrations not supplemented by description were regarded as valid.

4. Lymphocytes and the brain have been omitted purposely from generic consideration since the writer doubts their value in generic distinction.

5. In certain cases, statements known to be true for some of the species of a genus have been incorporated in the generic description since they represent all that is known at present about the features mentioned. Re-examination of the other species will decide whether such features will remain valid.

6. When the usual generic characters are not mentioned in the descriptions, such omission is taken to mean that no information is available, rather than that they are absent.

7. There have been incorporated into the genus descriptions certain features which may prove later to be specific characters, as for example, when structures are indicated as "present and absent." This is done largely for the sake of record and to indicate divergences from the former descriptions. It remains for future investigation to make the final disposal.

8. The term *chylus cell* is used to indicate the large, intestinal cells each of which is characterized by a longitudinal, intracellular canal. In the region involved, chylus cells usually alternate with the ordinary epithelial cells which line the lumen of the intestine.

9. Eisen's system of classifying the various forms of penial bulb has been followed to considerable extent. There is increasing evidence that the features of the penial bulb have distinct generic value.

10. No attempt has been made to list more than the most important literature involved in making this review. A complete set of references and a statement of the synonymy up to 1900 is given in Michaelsen's monograph.

SUBFAMILIES

Some attempts have been made in the past to establish subfamilies in the Enchytraeidae. Eisen (1905, pp. 11–13) proposed four subfamilies, *Mesenchytraeinae*, *Enchytraeinae*, *Achaetinae*, and *Lumbricillinae*, the major basis of distinction being the character of the penial bulb. However, since the structure of the penial bulb was not known for certain genera, the distribution of the genera among these subfamilies was to some extent inferential. Čejka (1910, p. 25) made use of three subfamilies under the names *Fridericiinae*, *Mesenchytraeinae* and *Henleinae*.

There seem to be some good grounds for considering the structure of the penial bulb as a basis for the erection of subfamilies, but since its structure is unknown in such genera as *Achaeta*, *Distichopus*, *Chirodrilus*, and *Stercutus*, it does not seem profitable just now to attempt to discuss this problem.

THE PENIAL BULB

The first attempt to use the characters of the penial bulb in the classification of the Enchytraeidae was made by Eisen (1905, pp. 6–10) who, after an extensive study of a large number of North American species, thought it possible to recognize three distinct "types" which were definitely related to certain taxonomic groups. The writer (Welch, 1914, pp. 173–180) presented a critical discussion of this matter, pointing out that it seemed necessary to make some modifications in Eisen's original system. Since that time many more of the North American forms have been studied and while it is still probable that certain changes may ultimately be necessary, all of the evidence at hand indicates that the characters of the penial bulb are valuable in generic and possibly in specific diagnoses. For this reason, statements as to the penial bulb have been incorporated into revised definitions of the various genera, retaining Eisen's terms for the different types. If many of the species from the Old World can be re-examined and the structure of the penial bulb described and figured, the taxonomic status of this organ will be made more certain.

For sake of ready reference, Eisen's summary of the three types of penial bulbs will be quoted here.

"The Mesenchytræid bulb is a single muscular structure, containing circular muscles as well as fan-shaped muscular bands connecting the body wall with the periphery of the bulb. Between the muscular bands are generally found numerous penial glands which open on the surface of the bulb around the penial pore. The spermaduct penetrates the bulb, opening on the center of its outer surface.

The Enchytræid bulb is multiple, consisting of several separate cushions grouped around the penial pore. In these cushions we find several sets or fascicles of glands, each fascicle opening by itself on the surface of the body. There are no muscular bands connecting the base of the cushions with its periphery. The sperm-duct never penetrates the bulbs or cushions but opens close to and independently of them. Exterior to the cushions there are numerous muscles connecting the body wall immediately surrounding the pore with other parts of the same somite.

The Lumbricillid bulb is always single and covered with a strong muscular layer, which however never penetrates down between the cells of the bulb. There are generally two or three distinct sets of glandular cells in the bulb. Some of these open in the lower part of the sperm-duct, or rather in a narrow groove in the elongation of the sperm duct. Others open on the free surface of the bulb, either irregularly or in narrow circular fields, bunched into fascicles. The sperm-duct penetrates one side of the bulb. In *Bryodrilus* the gland which opens in the extension of the sperm-duct is covered with a thin cushion of muscular strands, forming a bulb within a bulb."

RELATIONSHIPS

It is not intended that any particular significance be attached to the order in which the different genera are treated in this paper. Certain genera are too poorly known at present to justify any attempt to establish relationships, while others are little enough known to make it a difficult and an uncertain task. It thus seems best in this paper to omit efforts to determine phylogeny.

PROPAPPUS MICHAELSEN

Setae sigmoid; distal extremity cleft; those of a bundle equal; four bundles per somite, two lateral and two ventral. Dorsal pores absent. Oesophagus passing abruptly into intestine in 8; intestinal diverticula absent; chylus cells absent; peptonephridia absent. Origin of dorsal blood-vessel anteclitellar or intraclitellar. Nephridia with small, slender, funnel-shaped anteseptal part and with loose, scantily lobed, irregularly folded postseptal body, the folds being but little more than in close contact. Testes undivided; moderately compact. Spermiducal funnel extremely short; shallow bowl-shaped. Sperm duct very short; confined to 12. Penial bulb absent; small atrial chamber at ectal end of sperm duct; atrial glands absent. Spermathecae simple; no diverticula; no connection with digestive tract; long, extending into 6–12.

DISCUSSION

Formerly, the genus *Henlea* (Michaelsen, 1903, p. 51) was regarded as the most primitive group of the Enchytraeidae because of the diverse character of the setae manifested by the various species although it presented no distinct transition features leading into the near-standing, more primitive families of Oligochaeta (Phreodrilidae, Tubificidae, Naididae). In 1905, however, Michaelsen (pp. 24–28) described under the name ***Propappus*** a genus based upon specimens found abundant in Lake Baikal, Southern Siberia, at depths of 2–8 meters. These specimens presented a complex of characters of particular interest. Most of the fundamental features are enchytraeid leaving little doubt as to its membership in that group. However, certain affinities with other families are manifested in the presence of the following structures:

1. Cleft setae are recorded for the first time among the Enchytraeidae, all other known species having the simple-pointed type. Cleft setae are common in Naididae, Tubificidae, and Lumbriculidae.

2. The spermiducal funnel is a very short, shallow, bowl-shaped organ, resembling the funnel in certain other oligochaetes (*Tubifex*, et al) and showing little resemblance to the elongate, cylindrical, glandular, thick-walled funnel found in practically all enchytraeids. Apparently, only two other enchytraeids have spermiducal funnels which at all resemble those of ***Propappus***, namely, ***Mesenchytraeus bungei*** Mchlsn. and ***Mesenchytraeus grebnizkyi*** Mchlsn. (Michaelsen, 1901, pp. 193, 199), in which they are very short, and "pantoffelförmig."

3. Each nephridium consists of a small, slender, funnel-shaped nephrostome which constitutes the entire anteseptal part. The postseptal part, however, departs strikingly in form and structure from the typical enchytraeid condition in being very loosely constructed, having the appearance of an irregular knot of adherent loops

or folds, the free end of which composes the efferent duct. This type of nephridium recalls the postseptal coils in the same organ in Tubificidae, et al. Of all the other enchytraeids, *Mesenchytraeus* alone shows any approach to such nephridial structure, although its irregular, lobed, postseptal part in which the wide ducts are close together is definitely coalesced into one mass.

Only two species are known at present to belong to this annectent genus, namely, *glandulosus* and *volki*. The former, found in Lake Baikal, in the one on which the genus was established. Recently, Michaelsen (in a paper dated 1915 but which must have been published in 1916 since papers dated 1916 are referred to in it) described a second species, *volki*. It appears that this same writer first reported it in the "Hamburger Nachrichten, Jahrg. 1916, Nr. 53, vom 30, Januar, 3. Beilage, p. 1," as *Palpenchytraeus volki*, n. gen., n. sp. but later placed it in *Propappus*—a decision which certainly seems more nearly correct. It is worthy of mention that in this species the elongated spermathecae recall the condition in many of the North American mesenchytraeids.

HENLEA MICHAELSEN

Setae straight and unequal in size, or straight and equal in size, or slightly sigmoid and approximately equal in size; distal extremities simple-pointed; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus (with possible rare exceptions) expanding abruptly into intestine. Peptonephridia present or absent. Intestinal diverticula usually present. Origin of dorsal blood-vessel anteclitellar; rarely intraclitellar; cardiac body absent. Blood colorless. Nephridia with either large or small anteseptal part; nephridial canal loosely wound and surrounded by considerable amount of cell mass. Ventral glands absent. Testes compact; not divided. Spermiducal funnel cylindrical; sperm duct short, confined to 12, rarely longer. Sperm sacs and ovisacs absent. Penial bulb of lumbricillid type. Spermathecae connecting with digestive tract; diverticula present or absent.

DISCUSSION

Perhaps no genus of Enchytraeidae needs a thorough going revision as badly as does *Henlea*. Its heterogeneous nature has been recognized by investigators for some time but certain conditions surrounding the problem have thus far made such a revision almost impossible. It therefore presents many difficulties in connection with the present attempt to redefine the genus. Friend (1914b, pp. 150–153; 1915, pp. 197–198) has pointed out the existence of certain "groups" within this genus. The writer [Welch] suspects strongly that *Hepatogaster* Čejka should be regarded as a part of the genus *Henlea*—possibly as a subgenus. It seems likely that these "groups" will form the basis for the establishment of several subgenera when the genus is thoroughly worked over, particularly when many of the foreign species have been re-examined and more thoroughly described.

Certain deviations, apparent or otherwise, from the newly modified genus definition require some notice. Some ill-defined species (*lefroyi* Beddard; *scharfii* Southern; et al) seem to offer exceptional features, but the imperfect descriptions leave considerable doubt as to whether they belong in this genus at all. Hence no significance can be attached to them at present.

Eisen (1905, p. 98), in connection with his discussion of *Henlea*, presents the following statement: "Chylus cells in the intestine in the vicinity of clitellum." However, in his subsequent descriptions, no mention of them appears except in the case of *H. guatemalae* (pp. 102–103) which is described as having no chylus cells at all. In none of the American species of *Henlea* examined by the writer have chylus cells been observed.

A number of species have been described in which the origin of the dorsal blood-vessel is specified as intraclitellar and the definition has been modified so as to include these forms. However, Friend (1913b, pp. 460–461) has described a species under the name *insulae* which has the dorsal blood-vessel arising in "17/18 or 19/20." This form is assigned to *Henlea* but taking the original description as it stands, the writer is unable to place it with any more certainty in *Henlea* than in one or two other genera, as for example, *Enchytraeus*. For this reason, the apparent exception has not been given any particular consideration. *H. alba* (Friend, 1913c, p. 83) and *H. hillmani* (Friend, 1914b, p. 135) are reported as having the origin of the dorsal blood-vessel in the region of 13–14.

Of the sixty or more species now assigned to this genus, there are several which future investigations will certainly prove invalid.

HEPATOGASTER ČEJKA

Setae straight and equal; distal extremities simple-pointed; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia present, dorsal and ventral. Intestinal diverticulum present, surrounding digestive tract. Chylus cells absent. Origin of dorsal blood-vessel anteclitellar; cardiac body absent. Nephridia with small anteseptal part; nephridial duct loosely coiled and with distinct cell mass. Testes not divided. Spermiducal funnel cylindrical. Penial bulb of lumbricillid type. Spermathecae connecting with digestive tract; diverticula absent. Characteristic, longitudinal canals in epithelium of digestive tract in posterior part of body just entad of perivisceral blood-sinus.

DISCUSSION

The genus Hepatogaster was established by Čejka (1910) for the reception of two species which he considered as presenting characters representing a new group. A careful examination of descriptions reveals at least a close affinity with *Henlea*. In fact, it could be included in *Henlea* with practically no change in the limitations of the latter. Only one feature seems to offer any difference, namely, that the oesophagus passes gradually into the intestine, but it seems doubtful if a new genus could be established upon that character alone. The presence of certain peculiar longitudinal canals in the epithelium of the posterior part of the alimentary canal is stressed in the original description and while these characters seem to be unique, their value as a generic character remains to be demonstrated.

The structure of the penial bulb requires some notice. Čejka thought that it resembled the enchytraeid type, interpreting certain peculiar glands which open out through the body-wall in 12 and 13 in the vicinity of the sperm duct termination as parts of the penial bulb proper. Unfortunately, the penial apparatus is recorded in only one of the two species. However, a careful study of the description and Čejka's plates leads the present writer to hold that the bulb is of the lumbricillid type for the following reasons: 1. The sperm duct opens to the exterior through a compact, glandular bulb which is typically lumbricillid. This duct actually opens out through it into a penial invagination—a thing which does not occur in the typical enchytraeid bulb. (2) Of the nearby groups of problematical glands, the one in 12 is single and median, thus apparently belonging to neither bulb. (3) The other glands are in 13—another somite—a thing which has not been observed in connection with the various parts of a typical enchytraeid bulb. (4) In general appearance these peculiar glands resemble the "ventral glands" found in certain enchytraeids although they are unusual in being free from direct connections with the ventral nerve cord.

Owing to the incompleteness of some of the data on this proposed genus, it is allowed to stand for the present although there seem to be good reasons for believing that it should be reduced at least to the rank of a subgenus of *Henlea*.

BRYODRILUS UDE

Setae slightly or distinctly sigmoid; distal extremities simple-pointed; those of a bundle equal in size; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia present. Four intestinal diverticula present. Origin of dorsal blood-vessel intraclitellar; cardiac body present or absent. Nephridia with small anteseptal part; nephridial canal loosely wound; cell mass large. No ventral glands. Testes compact; not divided. Spermiducal funnel cylindrical; sperm duct confined to 12. Sperm sacs and ovisacs absent. Penial bulb of lumbricillid type. Spermathecae connecting with digestive tract; diverticula absent.

Discussion

While a few slight modifications have been introduced into the description of this genus, no important comments are demanded here. No mention of intestinal diverticula appears in the description of *B. sulphureus* (Bretscher, 1904, p. 262) but since the material on which the description was based was immature, this omission may have no significance. The head pore in this same species is recorded as appearing on the tip of the prostomium.

Four species are assigned to this genus.

BUCHHOLZIA MICHAELSEN

Setae sigmoid; distal extremities simple-pointed; those of a bundle approximately equal in size; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus expanding abruptly into intestine. Peptonephridia present. Chylus cells absent. Origin of dorsal blood-vessel anteclitellar or intraclitellar; arising from summit of dorsal intestinal diverticulum; cardiac body absent. Blood colorless. Nephridia with anteseptal part large or small. Spermiducal funnel cylindrical; sperm duct confined to 12. Structure of penial bulb unknown. Spermathecae connecting with digestive tract; diverticula absent.

DISCUSSION

In *Buchholzia focale* (Friend, 1914a, pp. 118–119) no mention is made of a dorsal intestinal diverticulum and the origin of the dorsal blood-vessel is given as "Henlean."

But little is known concerning the penial bulb in representatives of this genus. Eisen (1905, p. 12) places the genus under his subfamily Lumbricillinae but explains (p. 6) that he does so on account of its "undoubted relationship to the genus *Henlea.*"

Buchholzia parva (Bretscher, 1900a, p. 24) is described as showing no connection of the spermathecae with the digestive tract. However, the sexual maturity of the material might be questioned since it is stated that no trace of a clitellum was found.

Six species are now assigned to this genus.

MARIONINA MICHAELSEN

Setae sigmoid; distal extremities simple-pointed; those of bundle approximately equal in size; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia absent. Intestinal diverticula absent. Chylus cells absent. Origin of dorsal blood-vessel postclitellar; cardiac body absent. Blood red, yellow, or colorless. Nephridia with anteseptal part large or small; nephridial canal loosely wound; cell mass large. Ventral glands present or absent. Testes undivided. Spermiducal funnel cylindrical; sperm duct confined to 12. Sperm sacs present or absent. Penial bulb of the lumbricillid type. Spermathecae with or without connection with digestive tract; never greatly elongate; diverticula present or absent.

DISCUSSION

In a few species, assuming that they are correctly referred to this genus, there seems to be some deviation as to the origin of the dorsal blood-vessel. Bretscher (1900b, p. 449; 1901, pp. 209–10) described *rivularis* and *guttulata* as having this origin anteclitellar, and Eisen (1905, p. 91) reported it in 12 in the single specimen of *alaskae* which he described although he retained the general generic character of a postclitellar origin (p. 90).

Friend (1912a, p. 224) has described a species, *sialona*, which he assigns to *Marionina*, pointing out at the same time that it is strikingly like an *Enchytraeus*. This species possesses peptonephridia—a feature not represented in *Marionina* and *sialona* is unique in that respect if it actually belongs in *Marionina*. However, the writer has been unable, on the basis of the original description, to see why that species should not be assigned to *Enchytraeus*, rather than to *Marionina*. If this be the proper disposal of *sialona*, then the absence of peptonephridia still stands as an invariable character of the genus.

Eisen (1905, p. 90) held that a generic character appears in the presence of a small sperm sac in connection with each testis. Whether this is true, remains to be determined by future investigations.

In *antipodum* (Benham 1904b, p. 294) the body of the penial bulb appears to be of the lumbricillid type, but it is unique in possessing a single, large accessory gland. Bretscher (1901, p. 210) recorded *guttulata* as "ohne Prostata," but the whole description is so brief that it is impossible to judge accurately as to the sexual maturity of the material studied, or as to the exact meaning of the above quoted statement.

M. werthi Mchlsn. (1908, p. 15) has a penial bulb which is described as "einen winzigen, zwiebelförmigen, ganz in der Leibeswand verborgenen Bulbus aus. An diesen Bulbus, der manchmal als winzige äussere Papille etwas heraustritt, sitzt eine schwach gelappte, in die Leibeshöhle hineinragende Prostata."

About twenty-eight species are referred to this genus.

LUMBRICILLUS ÖRSTED

Setae sigmoid; distal extremities simple-pointed; those of a bundle approximately equal in size; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia absent. Intestinal diverticula absent. Chylus cells absent. Origin of dorsal blood-vessel postclitellar, rarely intraclitellar; cardiac body absent. Color of blood yellow, red, or colorless. Nephridia with anteseptal part either large or small; nephridial canal loosely wound, and considerable cell mass between the folds. Ventral glands present or absent. Testes divided deeply, forming a number of distinct lobes. Spermiducal funnel cylindrical; sperm duct long but confined chiefly to 12. Sperm sacs and ovisac absent. Penial bulb of lumbricillid type. Spermathecae connecting with digestive tract; diverticula absent.

Discussion

While the limits of this genus have been but little changed, certain variations may well be mentioned here. *L. viridis* (Stephenson, 1911, p. 48) has the dorsal blood-vessel arising in 13 and in *tuba* (p. 43) it arises in 13, 14, 15. A variety (?) of *minutus* (Müll.) described by Michaelsen (1911, pp. 1–4) has this vessel arising in 12. *Lineatus* (Müll.) (= *agilis* Moore) has also been described by some authors as having the dorsal vessel arising in 13.

Ventral glands do not appear in all representatives of *Lumbricillus*. Furthermore, they are said to occur in a few species of certain other genera (Welch, 1914, p. 141).

Distinct sperm sacs and ovisacs appear to be absent in this genus. A few references to very diminutive ovisacs restricted to the clitellar region occur in the literature (Eisen, 1905, p. 77; Moore, 1905, p. 397) but these can scarcely be regarded as having any special significance. Eisen (1905, pp. 75–76) stated that each division of the testes is capped by a small sperm sac and evidently regarded this as a generic character.

Stephenson (1911) has pointed out the close relation of *Lumbricillus* to *Enchytraeus* on the basis of the discovery of certain species which though assigned to the former, possess some characters strongly suggestive of the latter.

About thirty species are assigned to this genus at present, although there is reason for doubting the validity of some of them.

FRIDERICIA MICHAELSEN

Setae straight or nearly so; unequal, those in bundle developed in pairs, outer pair being largest, and enclosing smaller pairs; distal extremities simple-pointed; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores present. Oesophagus merging gradually into intestine. Peptonphridia present. Intestinal diverticula absent. Chylus cells present. Origin of dorsal blood-vessel postclitellar or intraclitellar, usually the former; cardiac body absent. Blood colorless. Nephridia usually with large anteseptal part, always consisting of more than nephrostome; cell mass well developed. Ventral glands usually absent. Testes not divided. Spermiducal funnel cylindrical; sperm duct short, usually confined to 12. Sperm sacs and ovisacs absent. Penial bulb of lumbricillid type. Spermathecae usually connecting with digestive tract; diverticula present or absent.

Discussion

While it seems advisable to make but little modification in the description of *Fridericia*, a few variations as recorded in the literature demand notice here.

F. tusca and *F. valdarnensis* are described by Dequal (1914, pp. 15, 17) as having setae which are sigmoid but those of a bundle are of unequal length, the inner ones being shorter. The description is very meager but it appears that even though they be sigmoid, they still resemble the typical *Fridericia* arrangement and development. Stephenson (1915, p. 47) describes the setae of *F. carmichaeli* as being of the "*Enchytraeus type*" but it may be that since in this species there are usually only two setae per bundle and since the outer setae of a *Fridericia* bundle are straight and approximately the same size, this statement could be true, although if more were present per bundle the inner ones might be shorter, smaller, and arranged in pairs. Friend (1912b, p. 24) states that the head pore in *F. anglica* occurs on the tip of the prostomium. In *Fridericia peruviana*, Friend (1911, pp. 734–736) described the oesophagus as passing abruptly into the intestine, but since the specimens on which the description was based were immature, it seems best to attach no particular significance to this case. According to Southern (1909, p. 165) *F. magna* Friend has bright red blood. Friend (1899, p. 263) stated that in *F. magna* an ovisac is present, extending caudad to 16.

At present about 90 species are assigned to *Fridericia* and while it is very possible that some of them are not valid, it appears that this is the largest of all the enchytraeid genera.

DISTICHOPUS LEIDY

Setae in two bundles per somite, representing the ventral rows only; nearly straight; simple-pointed but blunt; very stout and swollen in middle; hooked at proximal end. Head pore at 0/1. Oesophagus merging gradually into intestine. Peptonephridia present. Origin of dorsal blood-vessel postclitellar; small cardiac body present. Blood colorless. Nephridia with small anteseptal part. Spermiducal funnel cylindrical; sperm duct short, confined to 12. Penial bulb of lumbricillid type. Spermathecae not described.

DISCUSSION

The genus *Distichopus* is known only from a single set of specimens collected in Delaware and Pennsylvania by Leidy (1882, pp. 146–147). Some of these specimens were later studied by Moore (1895, pp. 754–756) who extended the account, although even yet too little is known concerning this unusual form. Certain important structural features, such as the spermathecae, are yet undescribed and thus the relationships of this genus are difficult to determine. Moore holds that it is a close ally of *Fridericia*. The single known species bears the name *silvestris*.

ACHAETA VEJDOVSKY

Setae entirely absent; dorsal and ventral rows preserved in some species only as pear-shaped gland cells in body-wall, gland cells also absent in other species. Head pore large; on tip of prostomium. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia present or absent. Origin of dorsal blood-vessel anteclitellar. Blood colorless. Nephridia with moderate or large anteseptal part. Spermiducal funnel cylindrical; sperm duct short or long but confined to region of clitellum. Penial bulb present; structure practically unknown; probably of lumbricillid type. Spermathecae with or without connection with digestive tract; diverticula absent.

Discussion

Achaeta is a small genus to which is assigned, at the present time, eight species, none of which occur in the Western Hemisphere. Its most striking characteristic is the total absence of setae. In most of the species, specialized, pear-shaped seta-glands occur in the positions where setae would be expected, although three species, *vejdovskyi* Bretscher (1902, p. 27), *maorica* Benham (1904a, pp. 221–223) and *camerani* (Cognetti 1899, pp. 1–4) are described as being completely devoid of seta-glands. Peptonephridia have not been found in *minima* Southern (1907, p. 77) and *incisa* Friend (1914b, pp. 133–134) but occur in the other known species. The penial bulb is practically unknown for this group since in no case is it described in adequate detail. It was figured by Vejdovsky (1879, pl. I, fig. 11) for *eisenii* but even there it is difficult to determine its exact composition. It suggests the lumbricillid type of bulb. In *maorica* Benham (1904a, p. 222) the spermathecae are greatly elongated, extending to 9 or 10, thus recalling the greatly elongated spermathecae of some of American species of *Mesenchytraeus*.

ENCHYTRAEUS HENLE

Setae straight; those of a bundle equal; distal extremities simple-pointed; four bundles per somite, two lateral and two ventral. Head pore at 0/1. Dorsal pores absent; Oesophagus merging gradually into the intestine. Peptonephridia present or absent. Intestinal diverticula absent. Chylus cells absent. Origin of dorsal blood-vessel postclitellar or intraclitellar; cardiac body absent. Blood usually colorless. Nephridia with small anteseptal part; cell mass well developed. Ventral glands sometimes present. Testes not divided. Spermiducal funnel cylindrical; Sperm duct confined to 12, or quite long, extending caudad through several somites. Sperm sacs present or absent. Penial bulb of enchytraeid type. Spermathecae connecting with digestive tract; diverticula present or absent.

Discussion

While it has been necessary to modify the older definition of the genus, only a few points require mention here. *E. dubius* (Stephenson, 1911, p. 56) is unique in possessing testes which are divided very much as is the case in representatives of the genus *Lumbricillus*. However, Stephenson himself (1915, p. 43) indicates that there is some doubt as to the generic position of this species. The same writer (1915, pp. 43–44) gives a critical discussion of sperm sacs in the genus *Enchytraeus* but makes no attempt to draw a general conclusion. Since the matter of sperm sacs is still in doubt, it seems best, in this paper, to use the data directly from the original descriptions and consider the statements of absence of sperm sacs as valid until they are definitely shown to be in error. The writer (Welch, 1914, pp. 177–178) previously discussed the penial bulb as a generic character and pointed out that not all of the species included in *Enchytraeus* conform to the enchytraeid type of bulb. However, it appears at this time that in the cases in which the penial bulb has been adequately described the large majority have bulbs of the enchytraeid type as proposed by Eisen and may so be incorporated into a revised statement of the limits of the genus, at least until subsequent investigation yields more complete data.

Eisen (1905, p. 61), in his generic description, states that the intestine generally possesses chylus cells. However, no mention of these cells is made later in his descriptions of species.

A genus, *Litorea*, described by Čejka (1913) for the reception of a species which he called *krumbachi*, is certainly the same as *Enchytraeus* and is so treated in this paper.

About thirty-five species are considered as belonging to this genus at the present time.

MICHAELSENA UDE

Setae straight; distal extremity simple-pointed; one to two setae per bundle, often but one; four bundles per somite, two lateral and two ventral; present only on some of the somites (except in *M. mangeri* Mchlsn.). Head pore at 0/1. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia present or absent. Intestinal diverticula absent. Origin of dorsal blood-vessel postclitellar; cardiac body absent. Blood colorless. Nephridia with small anteseptal part, consisting of nephrostome only. Ventral glands absent. Testes not divided. Spermiducal funnel cylindrical; sperm duct confined to 12, or long and extending caudad to 14. Penial bulb of the enchytraeid type. Spermathecae connecting with digestive tract; diverticula absent.

DISCUSSION

Formerly the absence of setae from some or the majority of the somites was regarded as one of the chief distinguishing features of this genus but Michaelsen (1914, pp. 177–181) described a new species under the name *mangeri* in which setae are present in four bundles on all of the somites. This species may be regarded as a connecting form between *Michaelsena* and *Enchytraeus* and at the same time, according to Michaelsen, emphasizes the relation of *Michaelsena* to *Fridericia*.

Southern (1913, pp. 8–12) described under the name *Grania* what he regarded as a new genus, pointing out similarities with a form then known under the name of *Enchytraeus monochaetus* Mchlsn. The latter is now known to belong to *Michaelsena* and *Michaelsen* (1914, p. 181) seems to be right in placing *Grania* there also.

Eisen (1905, p. 73) incorporated in his definition of this genus the statement that there are "No penial bulbs," but this seemed to be based upon the condition which he found in a single specimen to which he gave the name *paucispina* and which did not permit a full descripctiption. However, the descriptions of species now assigned to *Michaelsena* indicate that it may be of the enchytraeid type. Eisen (1905, p. 11) placed the genus in his subfamily *Enchytraeinae*.

It seems to be becoming increasingly difficult to separate *Michaelsena* from *Enchytraeus* and it is possible that some future revision based upon more intensive study of all of the species involved may suggest the fusion of the two groups.

Eight species are assigned to this genus at present.

MESENCHYTRAEUS EISEN

Setae sigmoid; distal extremities simple-pointed; approximately equal in size in bundle; four bundles per somite, two lateral and two ventral. Head pore distinct; usually at or very near tip of prostomium. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia absent. Intestinal diverticula absent. Chylus cells absent. Origin of dorsal blood-vessel postclitellar; cardiac body present. Blood either colorless or red. Nephridia with small anteseptal portion, consisting merely of nephrostome; postseptal part large, irregularly pluri-lobed, and with cell mass between folds of closely wound nephridial canal greatly reduced. Ventral glands absent. Testes compact; undivided. Spermiducal funnel usually cylindrical; sperm duct short and confined to 12, or very long extending caudad for many somites. Sperm sacs and an ovisac often present. Penial bulb of mesenchytraeid type. Spermathecae confined to 5, or elongated and extending caudad for varying distances, sometimes to clitellum; diverticula present or absent; communication with digestive tract present or absent.

DISCUSSION

Eisen (1905, p. 14) stated that a "single median ovisac" and "one pair of sperm-sacs generally of large size" are present in *Mesenchytraeus*. However, *Mes. altus* Welch (1917, p. 71), which unquestionably belongs to this genus, has a *pair* of ovisacs and it seems possible that other cases of that sort will appear.

Several special cases which depart somewhat from the definiton as proposed require mention here. In *eastwoodi* Eisen (1905, p. 50) the head pore occurs on the upper side of the prostomium near 0/1. *Mes. mencli* Vejd. (1905, p. 5) is described as having "Herz im 12," apparently referring to an intraclitellar origin of the dorsal blood-vessel. A similar origin seems true of *celticus* Southern (1909, p. 155), although the statement is not made positively. Bretscher (1902, p. 16) claimed that specimens of *setosus* Mchlsn. (=*megachaetus* Bret.) show the dorsal blood-vessel arising in 11, 13, or 16 — which seems an unusual variation. *Mes. grandis* Eisen (1905, p. 44) is described as having nephridia with broad anteseptal parts. In *orcae*, *mirabilis*, and *kincaidi* (Eisen, 1905, pp. 40–41), the testes are recorded as composed of "lobes" but it is not clear whether they are deeply divided as in the case of *Lumbricillus* or are merely lobulate at the free extremity. Bretscher (1901, p. 212) states that in *alpinus* the spermiducal funnel is in 8, but nothing is given concerning the sperm duct. In *nanus* (Eisen, 1905, pp. 51–52), the penial bulb is described as absent, but there seems to be some possibility that immature specimens were studied.

This genus contains at the present time about 50 species.

HYDRENCHYTRAEUS BRETSCHER

Setae sigmoid; distal extremities simple-pointed; four bundles per somite, two lateral and two ventral. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia present. Origin of dorsal blood-vessel postclitellar. Blood yellow or red. Nephridia with large or small anteseptal part. Spermiducal funnel cylindrical. Spermathecae without diverticula.

Discussion

This genus was established by Bretscher (1901, pp. 208–209) for two incompletely described species, *stebleri* and *nematoides*, found in Switzerland. Its status is somewhat uncertain owing to the fact that information on the head pore, relation of oesophagus to intestine, chylus cells, cardiac body, ventral glands, testes, sperm sacs, ovisacs, penial bulb, and relation of spermathecae to the digestive tract is entirely lacking. Likewise certain other features are incompletely described. Since the original description is the only record, nothing further can be done with these forms until specimens are again found and studied critically. The fragmentary information which is available seems to indicate that it is a valid genus.

STERCUTUS MICHAELSEN

Setae sigmoid; distal extremity simple-pointed; four bundles per somite, two lateral and two ventral. Head pore absent (apparently) or very small. Dorsal pores absent. Oesophagus merging gradually into intestine. Peptonephridia absent. Intestinal diverticula absent. Chylus cells absent. Origin of dorsal blood-vessel anteclitellar; cardiac body present. Blood colorless. Nephridia with small anteseptal part consisting of but little more than a mere nephrostome; postseptal part large; nephridial canal loosely wound and surrounded by considerable cell mass. Testes small; undivided. Spermiducal funnel short and distinctly funnel-shaped. Penial bulb unknown. Spermathecae not connected with digestive tract; diverticula absent.

Discussion

The genus *Stercutus* was established by Michaelsen (1888) to receive a species, *niveus*, which was found inhabiting fish excrement in Germany. No other representatives of this genus have ever been described. Lack of information as to the character of the penial bulb, the sperm duct, and the presence or absence of ventral glands, ovisacs and sperm sacs gives some difficulty in determining the affinities of this genus.

CHIRODRILUS VERRILL

Setae in six bundles per somite, two sub-dorsal, two lateral, and two ventral; those in ventral and lateral bundles distinctly sigmoid, those in sub-dorsal less curved; distal extremities simple-pointed. Blood colorless.

Discussion

The description of this interesting genus is extremely meager and based entirely upon the original record by Smith and Verrill (1871, pp. 450–451) in which but few of the important details are described. Two species are assigned to this genus, *larviformis* and *abyssorum*, both collected in Lake Superior. Both are apparently deep water forms, *larviformis* being dredged from depths of 17 and 59 fathoms, and *abyssorum* from 47 and 159 fathoms. There is some question as to the position of this genus, certain previous writers having regarded it as a tubificid. Beddard (1895, p. 314) and Michaelsen (1900, p. 88) have classed it among the Enchytraeidae, although the latter (1903, p. 50) later placed it among the Tubificidae. Eisen (1905, p. 13) retains it in the Enchytraeidae. It is unlikely that the matter can receive any positive decision until material is again secured and carefully studied. Since some of the characters as described are apparently enchytraeid in nature, it is included in this review, with the realization, however, that future investigation may show it to have other affinities. If it be an enchytraeid, it is unique for the entire family in possessing six sets of setae per somite. Eisen (1905, p. 13) places it under the Lumbricillinae, but states (p. 6) that it is "appended for convenience sake" and points out correctly that nothing is known concerning the penial bulb and other internal structures.

GENERA DUBIA

Under the name *Chamaedrilus,* Friend (1913a, pp. 260–263) described a new genus from material collected in England. Considering the generic characters as recognized at present for the family Enchytraeidae, a careful comparison has made it impossible for the writer to distinguish *Chamaedrilus* from *Marionina* and in this paper they are regarded as the same.

Bretscher (1905) described what he regarded as a new genus of Enchytraeidae under the name of *Euenchytraeus* but unfortunately the record was made on sexually immature material and as a consequence nothing could be determined as to the nature of the reproductive organs. Since no further record of this postulated genus occurs in the literature and since the original description is unusable as it stands, it is omitted from consideration in this paper.

KEY FOR THE IDENTIFICATION OF THE GENERA OF ENCHYTRAEIDAE

1 (2) Setae entirely absent; represented in most species only by four longitudinal rows of pear-shaped glands in body-wall .... *Achaeta*

2 (1) Setae present 3

3 (4) Setae arranged in two bundles per somite ...... *Distichopus*

4 (3) Setae arranged in more than two bundles per somite 5

5 (6) Setae arranged in six bundles per somite, two subdorsal, two lateral, and two ventral .... *Chirodrilus*

6 (5) Setae arranged in four bundles per somite, two lateral and two ventral 7

7 (8) Setae cleft at distal extremities; spermiducal funnel wide, open, shallow, and extremely short; postseptal part of nephridia composed of a few coherent folds not intimately fused, forming very loose organ .... *Propappus*

8 (7) Setae simple-pointed at distal extremities; spermiducal funnel cylindrical or trumpet-shaped; postseptal part of nephridia compact 9

9 (10) Setae straight, arranged in pairs, inner pairs of bundle successively smaller than outer; dorsal pores present; chylus cells present in walls of intestine .... *Fridericia*

10 (9) Setae straight, sigmoid, or in pairs in bundle with smaller ones within; dorsal pores absent; chylus cells absent from walls of intestine....................................11

11 (14) Oesophagus expanding abruptly into intestine...........12

12 (13) Dorsal blood-vessel arising from anterior end of single, dorsal intestinal diverticulum......................*Buchholzia*

13 (12) Dorsal blood-vessel arising directly from perivisceral blood-sinus.. *Henlea**

14 (11) Oesophagus merging gradually into intestine............15

15 (16) Setae usually absent from several somites (except in *Michaelsena mangeri* Mchlsn.); usually one setae per bundle, never more than two............................*Michaelsena*

16 (15) Setae regularly present on all somites except first and last and possibly the clitellar.............................17

17 (20) Intestinal diverticula present.........................18

18 (19) Setae sigmoid; four distinct intestinal diverticula; origin of dorsal blood-vessel intraclitellar..............*Bryodrilus*

19 (18) Setae straight; one intestinal diverticulum completely surrounding digestive tract; origin of dorsal blood-vessel anteclitellar................................ *Hepatogaster*

20 (17) Intestinal diverticula absent.........................21

21 (22) Setae straight; those of a bundle equal........*Enchytraeus*

22 (21) Setae sigmoid....................................23

23 (24) Peptonephridia present................*Hydrenchytraeus*

24 (23) Peptonephridia absent..............................25

25 (26) Origin of dorsal blood-vessel anteclitellar; spermiducal funnel short and trumpet-shaped................*Stercutus*

26 (25) Origin of dorsal blood-vessel postclitellar; spermiducal funnel cylindrical....................................27

27 (28) Testes divided..........................*Lumbricillu*

28 (27) Testes solid, not divided...........................29

29 (30) Cardiac body absent; penial bulb of lumbricillid type; nephridial duct loosely coiled and cell mass of postseptal part well developed; spermathecae never extending through several somites.............................*Marionina*

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* A few species, e.g., *hillmani* Fr., *insulae* Fr., *marina* Fr., *alba* Fr., and three or four uncertain forms, have been assigned to *Henlea*, although they are described as having the oesophagus pass gradually into the intestine.

30 (29) Cardiac body present; penial bulb of mesenchytraeid type; nephridial duct closely wound and cell mass reduced to minimum.................................. *Mesenchytraeus*

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